

SPECIES DELIMITATION, AND NEW TAXA AND COMBINATIONS IN *LEUCAENA* (LEGUMINOSAE)

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INTRODUCTION

Different approaches to species delimitation have resulted in widely differing numbers of species recognized within *Leucaena* Benth. by different authors. This has been the main cause of taxonomic confusion within the genus. In this paper, species delimitation in *Leucaena* is discussed, one new species and two new subspecies are described, and four new combinations proposed. These are published here in advance of a forthcoming monograph (Hughes, in press) in order to expedite use of these new names in a series of imminent publications and databases concerned with economic use of the genetic resources of *Leucaena*, including the Oxford *Leucaena* seed database (Hughes, unpubl.), a *World Germplasm Catalogue* (Bray et al., unpubl.) and a *Genetic Resources Handbook* (Hughes, unpubl.). Full descriptions, specimen citation lists, drawings, and distribution maps are presented in the monograph, except for *L. lempirana*, which is fully described and illustrated here.

SPECIES DELIMITATION

Although the variation in numbers of species recognized and in the importance given to infraspecific ranks by different authors is partly attributable to the history of collection and species discovery, it is also a function of differing views about what constitutes good character evidence for species or infraspecific taxa. Britton and Rose (1928) recognized 39 species of *Leucaena* and based delimitations on characters that are now viewed as unreliable, either because they present continuous patterns of variation across species (e.g., leaf, leaflet, and pod dimensions) and are therefore not amenable to anything but arbitrary division, or because they vary within populations that are otherwise constant (e.g., leaf and pod pubescence). In the absence of rangewide sampling, they failed to detect the continuities and population variation that are now obvious and the result was a proliferation of supposed new species. Brewbaker and colleagues reduced the number of species initially to ten (Brewbaker et al. 1972; Brewbaker & Ito 1980) with gradual re-acceptance of additional species to 16 (Brewbaker 1987; Brewbaker & Sorensson 1994). The criteria they used to delimit species were never explicitly stated, and no formal taxonomic account was produced. It is clear, however, that Brewbaker maintained a skeptical view of the distinction of any species until he had collected material of it himself and observed its progeny in cultivation in the Waimanalo arboretum in Hawaii. Additional species were acknowledged only with some reluctance during the 20 years after his initial sweeping

reduction to ten. Zárate (1984, 1994), in his revision of the Mexican species, described two new species, four new subspecies, and proposed five new combinations, four of them based on species recognized by Britton and Rose. In so doing he adopted a third approach to species delimitation that relied on very extensive use of subspecies. Zárate (1994) justified this on the frequent occurrence of interspecific hybridization in *Leucaena*, and the unusual "abundance of incipient allopatric speciation" (Zárate 1994: 88), which he attributed to the complex biogeographical history of the region. Subspecies were viewed as a solution to these perceived difficulties. Zárate also apparently saw subspecies as a mechanism to indicate relationships reflected in his belief that "a classification exclusively of distinct species is of no benefit either to the interested scientist, or to communication of this knowledge to the user community" (Zárate 1994: 88, translated from Spanish). Zárate further mentioned ease of identification (to binomial) with certainty as more than compensating for the inconvenience caused by a system replete with trinomials.

The last 15 years has seen a dramatic renewal of interest in the nature of species, re-examination of traditional species concepts, development of new ones, and new methods to discover species, driven by the rise and adoption of cladistic methods and molecular evidence in systematics (reviewed by, e.g., Mishler & Budd 1990; Baum 1992; Panchen 1992; Rieseberg & Brouillet 1994; Davis 1995; Luckow 1995). Given this renewed debate, Luckow (1995) suggested that explicit justification for the species concept adopted and the criteria applied to delimit species should be a requirement for any taxonomic revision. My aim in delimiting species within *Leucaena* has been to name, as species, all the diagnosable entities based on available character evidence. Such an objective must emphasize distinctions rather than similarities, as pursued by Zárate (1994). To do this I have used the explicit pattern based species concept of Rosen (1979), Eldredge and Cracraft (1980), Nelson and Platnick (1981), and Cracraft (1983), recently re-defined by Nixon and Wheeler (1990: 218) as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals," and now widely known as the phylogenetic species concept. This concept uses populations as the units of analysis and looks for aggregations of populations that possess constant and unique character states or unique combinations of character states. A logical consequence of the phylogenetic species concept is that species are delimited by the same criteria used to define characters and character states in primary homology assessment for cladistic analysis. The advantage of the phylogenetic species concept over other morphological concepts such as the intuitive 'taxonomic' (species as the smallest groups that are consistently and persistently distinct as distinguished by ordinary means, Cronquist 1988), phenetic, or 'traditional' concepts, is that it provides explicit justification for decisions taken. One obvious limitation is that characters that do not show discrete states when the total variation within a genus is viewed simultaneously may be amenable to division when only two, or a small subset of species, are considered.

Definitions of 29 morphological characters and their character states which partition variation within *Leucaena* are presented in Hughes (in press). These character states provide the basis for delimitation of the 22 species recognized in the forthcoming monograph of *Leucaena* (Hughes, in press). This result means that many of the species recognized by Britton and Rose are treated as conspecific. In contrast, some of the subspecies recognized by Zárate (1994), and one described

by Hughes (1991), qualify as distinct species. While most of these are attributable to older names provided by Britton and Rose, two require new combinations proposed here. Although there is indeed evidence for interspecific hybridization within *Leucaena* (e.g., Hughes & Harris, 1994), infraspecific taxa provide no solution to that problem. Zárate's second contention that subspecies are an effective way to indicate groups of closely related taxa, is again little substitute for an informed analysis of species relationships and presentation of an explicit hypothesis of relationships in the form of a branching diagram (Hughes, in press). Zárate's justification, based as it was on process assumptions and scenarios, is a retreat from the morphological evidence. Furthermore, experience in other economically important forestry genera (e.g., *Pinus* L.) indicates a persistent reluctance to use trinomials in practice.

Application of the phylogenetic species concept has raised the question of the nature and reality, if any, of infraspecific taxa. Some have argued that the phylogenetic species concept denies the existence of infraspecific taxa (Rosen 1979; Donoghue 1985; Cracraft 1992). After all, if species are the smallest aggregations of populations diagnosable by a unique combination of character states, what can be the nature of infraspecific taxa? Again, this depends on the criteria used to define characters. Use of strict criteria that demand discrete, fixed differences among populations leaves a large body of evidence, largely from quantitative characters that show continuous variation, but are not amenable to objective partitioning based on absolute gaps. Use of this evidence, albeit using arbitrary divisions, provides a viable extension of the phylogenetic species concept to infraspecific level (Nixon & Wheeler 1990; Luckow 1995). I have used variation in a number of quantitative leaf and pod traits that were rejected as characters, because they vary continuously across species and show overlapping variation when viewed across the genus as a whole, to recognize six infraspecific taxa (Hughes, in press). Subspecies are used for entities which are distinguished by several quantitative traits and which are clearly correlated with geography. Varieties are used for entities which differ in several quantitative traits but which are not correlated with geography or for which the geographic limits of the variants are poorly known. On this basis two new subspecies are described here and two subspecies originally described by Zárate (1994) are demoted to varietal rank.

NEW TAXA AND COMBINATIONS

Leucaena lempirana C. E. Hughes, sp. nov.—TYPE: HONDURAS. YORO: 6 km SE of El Negrito, on side rd to Nueva Esperanza, nr Río Cuyamapa, on edge of Olomán Valley, 15°17'N, 87°40'W, 25 Feb 1991, *Hughes 1412* (holotype: EAP!; isotype: FHO! additional isotypes to be distributed to MEXU, K, NY). Fig. 1.

Species nova, *L. salvadorensi* proxima, sed foliis pinnis numerosioribus, pinnis foliolis numerosioribus minoribusque, ramulis capitula ferentibus terminalibus erectis, determinatis, aphyllis, in apicem vegetativum abortivum desinentibus differt.

Small slender tree 4–15 (–20) m tall, 10–40 cm bole diameter, typically with upright branching and a rounded crown above a short clear bole to 4 m. Bark light grey-brown with powdery orange-brown lenticels and shallow rusty orange-brown vertical fissures, inner bark green. Leafy shoots terete, pale orange-brown

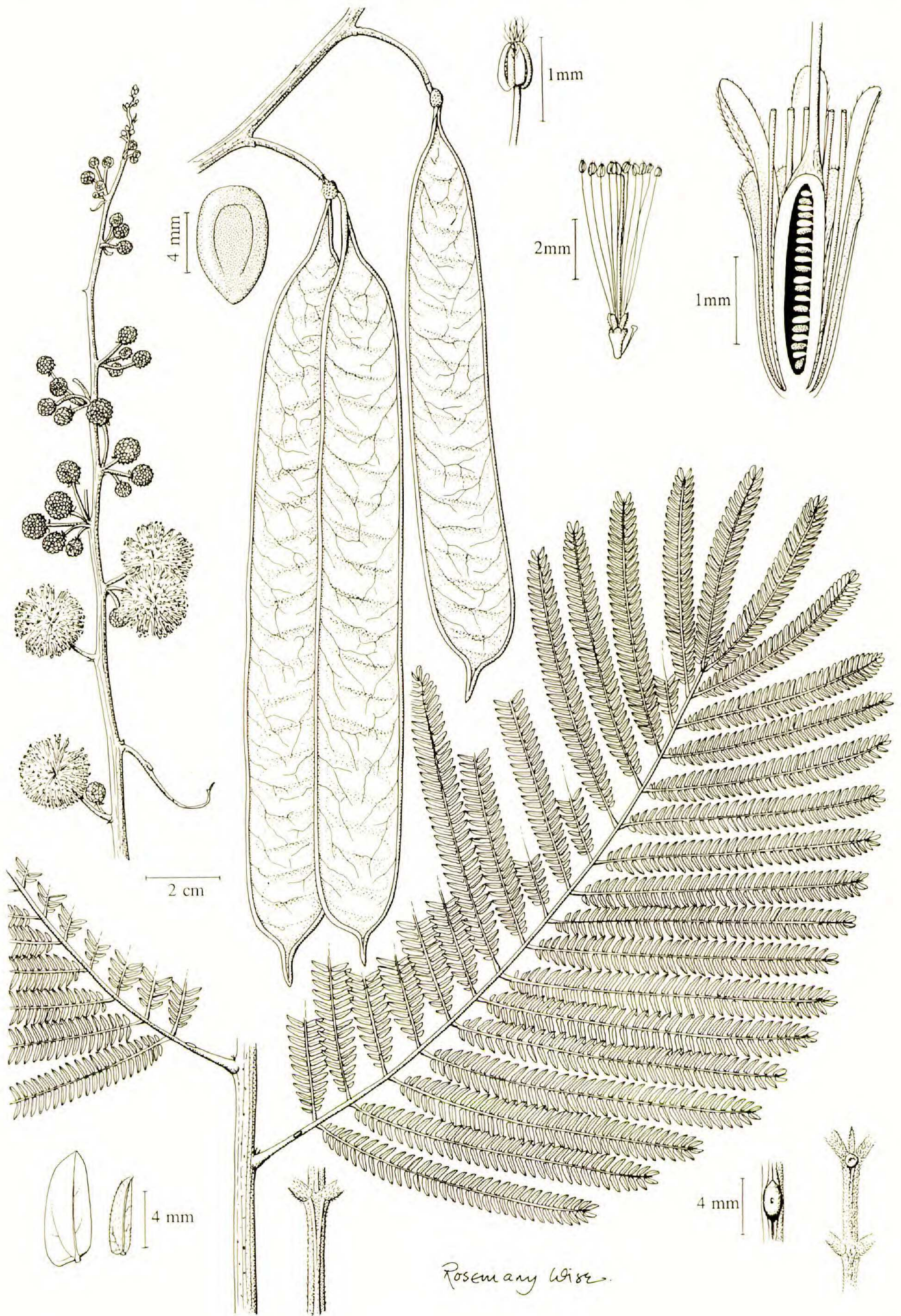


FIG. 1. *Leucaena lempirana*. Leaf, pod, flowering shoot, petiolar and rachis nectaries, leaflet, flower with peltate bract, seed, longitudinal section of flower and anther. (Based on: *Hughes 1412*, FHO, isotype.)

striped pale grey-brown covered in fine whitish velutinous pubescence. Stipules subulate with small asymmetric wings at base, hairy, 3.5–3.8 mm long, persistent. Leaves 19–24 (–26) cm long, 11–14 (–19) cm wide, petioles (including pulvinus) 25–35 mm long, one or occasionally two pale yellow to orange-yellow, sessile, elliptic dome-shaped or truncate-conic nectaries, 3×1.5 mm, at distal end on adaxial side of petiole; rachis 11–15 cm long with two narrow adaxial ridges and a small elliptic conic nectary, 1×0.7 mm, at distal end, extending beyond the terminal pair of pinnae as a short pointed hairy mucro, 2.5–3.5 mm long, curling when dry; pinnae 14–19 pairs; pinnular rachis 7–10 cm long, densely covered in short white hairs, with a minute round nectary at distal end; leaflets (27–) 30–36 (–40) pairs per pinna, nearly sessile, 5–6 mm long, 1.6–2 mm wide, asymmetric, oblong, obtuse to rounded apically, rounded to truncate basally, densely white-pubescent, midrib strongly asymmetric, a few secondary veins visible. Capitula 16–18 mm in diameter at anthesis, each with 100–130 pale cream-white flowers, in fascicles of 3–5 at nodes or in leaf axils on long erect terminal anauxotelic shoots on which leaf development is suppressed, the capitula exerted beyond the periphery of the tree crown; peduncles 12–25 mm long, angled, pale orange-brown with velutinous white pubescence and an involucre of bracts. Flowers subtended by peltate bracts, 2.2–2.6 mm long, 0.6–0.9 mm in diameter, densely pubescent; calyx 2.4–2.7 mm long, glabrous, pale cream, the lobe tips tinged green; petals free, 3.5–4.5 mm long, glabrous, occasionally sparsely ciliate on lobe tips, pale green; filaments 10–12 mm long, white; anthers with a tuft of terminal hairs, apiculum absent, cream-white; ovary 2.3–3.4 mm long, sessile, pale brown, densely covered in short white hairs, style 10–11 mm long, white, with a terminal tubular stigma. Pods (10–) 12–20 (–25) cm long, (18–) 20–26 (–32) mm wide, 1–2 (–3) per capitulum, pendulous on sturdy 8–11 mm long stipes, oblong to linear-oblong, constricted where seed abortion has occurred, apex mucronate with a beak 5–15 mm long, base cuneate, narrowly plano-compressed, 14–20 seeded, valves membranous, mid-orange-brown, pubescence variable from nearly glabrous to dense and velutinous, venation reticulate, most pronounced at margins, the margins slightly thickened, dehiscent along both sutures. Seeds 6.6–8.8 mm long, 3.8–5.2 mm wide, compressed, flattened, elliptic to ovate, deep chestnut-brown, glossy, aligned transversely in pods, pleurogram visible, deep U-shaped, symmetrical.

ADDITIONAL SPECIMENS EXAMINED. **Honduras.** YORO: W end of the lower Aguán Valley, rd W from Olanchito towards Sabana Larga, 1 km S of San Lorenzo, 15°25'N, 86°57'W, 25 Mar 1991, *Hughes 1447* (EAP, FHO, K, MEXU, NY); 3 km WSW of Arenal, rd to Jocón, lower slopes of hills S side of the Aguán Valley, 15°22'N, 86°51'W, 16 Feb 1991, *Hellin & Hughes 4* (EAP, FHO, K, MEXU, NY); 9 km SSE of Arenal, rd towards Jocón and Yoro, 15°22'N, 86°51'W, Feb 1989, *Alvarado G/2/89* (HEH); 15 km NW of Jocón, rd to the Aguán Valley in tributary valley of the Río Macora, between Macora and Sabana Larga, about 8 km NW of Macora, 15°21'N, 86°59'W, 17 Feb 1991, *Hellin & Hughes 14* (EAP, FHO, K, MEXU); rd E from Santa Rita to Yoro, 4 km E of Negrito immediately E of Valle Olomán above the Río Cuyamapa, 15°18'N, 87°40'W, 25 Feb 1991, *Hughes 1411* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, 3 km SE of El Negrito or 2 km NW of the Río Cuyamapa in the Valle Olomán, 15°18'N, 87°41'W, 25 Feb 1991, *Hughes 1414* (EAP, FHO, K, MEXU, NY); 0.5 km SW of San Lorenzo, N side of the Aguán Valley, 47 km W of Olanchito, 15°25'N, 86°58'W, 17 Feb 1991, *Hellin & Hughes 11* (EAP, FHO, K, MEXU, NY); 3 km S of Zapamatepe, 8 km W of Arenal, S side of the Aguán Valley, 15°22'N, 86°54'W, 16 Feb 1991, *Hellin & Hughes 7* (EAP, FHO, K, MEXU, NY); N side of the Aguán Valley between Medina and Coyoles, rd 12 km W of Olanchito, 15°28'N, 86°28'W, 17 Feb 1991, *Hellin & Hughes 8* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, nr Cuyamapa, 15°16'N, 87°27'W, 15 Feb 1991, *Hellin & Hughes 1* (EAP, FHO, K, MEXU, NY); Santa Rita, 5 km ESE of El Negrito, side rd off the main El Negrito to Yoro rd to Nueva Esperanza, banks of the Río Cuyamapa, 15°17'N, 87°40'W, 4 Aug 1991, *Hughes*

1479 (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, 4 km E of El Negrito, nr the turnoff over the Río Cuyamapa towards Morazán, 15°17'N, 87°39'W, 7 Mar 1992, *Hughes 1712* (E, FHO, K, MEXU, NY).

The first herbarium specimen of this new species (*Alvarado G/2/89*) was collected in 1990 by Gaspar Alvarado and Jon Hellin, foresters from the National Forestry School (Escuela Nacional de Ciencias Forestales), Siguatepeque, Honduras, and I thank them for drawing my attention to it. *Leucaena lempirana* is the only species of *Leucaena* endemic to Honduras and is named here in honor of the Indian chief Lempira, a Cacique from the Celaque region of Honduras, who was killed while attending a peace conference, the victim of a breach of truce imposed by the Spaniards (Wendell 1976) and after whom the Honduran currency is named. *Leucaena lempirana* is restricted to two areas, the Aguán Valley system and the valleys of Olomán and Cataguana, both in the Department of Yoro in northern Honduras.

Leucaena lempirana belongs within the *L. shannonii* J. D. Smith alliance with *L. shannonii*, *L. salvadorensis* Standl. ex Britton & Rose, and *L. magnifica* (C. E. Hughes) C. E. Hughes but shows closest affinities to *L. salvadorensis*. It is distinguished from *L. salvadorensis* by its long terminal anauxotelic flowering shoots on which the capitula and pods are borne on the periphery of the tree crown. These flowering shoots are strongly reminiscent of those of *L. shannonii*. It is distinguished from both *L. salvadorensis* and *L. shannonii* by its smaller and more numerous leaflets and pairs of pinnae per leaf. The pods are also similar to those of *L. shannonii* and are variably glabrous or pubescent as for that species. *Leucaena lempirana*, *L. salvadorensis*, and *L. shannonii* all occur in Honduras but occupy distinct and virtually allopatric distributions in different, isolated valley systems at low to middle elevations.

Leucaena macrophylla Benth. Bot. Voy. Sulphur. 90. 1844.—TYPE: MEXICO. Guerrero: Acapulco, 1841, *Hinds s.n.* (holotype: K!).

Britton and Rose (1928) distinguished *L. nelsonii* Britton & Rose from *L. macrophylla* solely by its copiously pubescent leaflets and had not seen fruiting material at the time of their original description. Zárate (1994) placed *L. nelsonii* as a subspecies of *L. macrophylla* based on quantitative leaf and pod differences and leaflet pubescence, and assigned material from SE coastal Guerrero (type locality of *L. nelsonii*), coastal Oaxaca, and Veracruz to that subspecies. The type specimen of *L. nelsonii* does indeed have copious pilose or villous pubescence on both leaflet surfaces, a feature also noted by McVaugh (1987) to be present on trees from throughout the Balsas region from eastern Jalisco to Guerrero. As noted by McVaugh (1987), even on typical representatives of *L. macrophylla* from the northern part of its range, leaflets are rarely completely glabrous, but often have stiff white hairs on the pulvinules and along the primary and secondary veins. Rangewide survey of leaflet pubescence reveals that while material from the Balsas region is generally more pubescent, it is variable, and pubescent individuals also occur elsewhere (e.g., coastal Michoacán). At the type locality of *L. nelsonii* leaflet pubescence also varies, as shown by some very sparsely pubescent individuals (e.g., *Hughes 644*). Material from coastal Oaxaca, assigned to subsp. *nelsonii* by Zárate (1994), is generally glabrous. Given this pattern of variation in leaflet pubescence and the close similarity of the material from coastal Guerrero

to typical examples of *L. macrophylla*, there appears to be no basis for maintaining *L. nelsonii* as a separate species or subspecies within *L. macrophylla*. The type specimen of *L. macrophylla* was collected from 'Acapulco'; given that there is no record of typical material of *L. macrophylla* from the immediate vicinity of Acapulco, it is probable that the type was collected either along the coast (near the type locality of *L. nelsonii*) or inland close to the route to Mexico City, further encouraging treatment of these two species as conspecific. Similar variation in leaflet pubescence has been noted within the other large-leaflet species *L. lanceolata* S. Watson and *L. trichodes* (Jacq.) Benth.

Material of *L. macrophylla* from coastal Oaxaca and Veracruz, placed in subsp. *nelsonii* by Zárate (1994), does however differ from typical representatives of *L. macrophylla* in leaf and pod dimensions, habit, and chloroplast DNA restriction site variation, and merits recognition as a distinct subspecies. Because the type of *L. nelsonii* belongs with *L. macrophylla* and not with the distinct Oaxacan material, there seems no alternative but to add a new subspecies, here named *istmensis*, to account for this variation, despite the additional confusion that this may cause. Subspecies *istmensis* differs from subsp. *macrophylla* in its smaller leaflets and pods, shorter peduncles, and in its cpDNA, by 16 autapomorphic fragment changes, six of which are unique (Harris et al. 1994).

Leucaena macrophylla Benth. subsp. **istmensis** C. E. Hughes, subsp. nov.—TYPE: MEXICO. Oaxaca: 40 km W of Puerto Escondido, coast rd to Pinotepa Nacional, nr San Isidro Llano Grande, 2 km inland from Pacific coast, 15°58'N, 97°10'W, 26 Mar 1989, *Hughes 1338* (holotype: FHO!; isotypes distributed to AAU, K, MEXU, NY).

A *L. macrophylla* Benth. subsp. *macrophylla* pinnis cujusque folii paucioribus, foliolis angustioribus, pedunculis brevioribus, leguminibus angustioribus differt.

Small, generally single-stemmed tree 3–10 (–15) m tall, bole 10–15 (–40) cm in diameter. Leaves: petioles (including pulvinus) 11–22 mm long, rachis (7–) 8.2–10.9 cm long; pinnae (2–) 3 pairs; leaflets (15–) 23–56 (–64) mm long, (6–) 17–24 (–28) mm wide, 3 or 4 (–6) pairs per pinna. Capitula 7–9 (–10) mm in diameter at anthesis; peduncles (3–) 4–10 mm long. Flowers subtended by small peltate bracts, 1.7–2.1 mm long; calyx 1.9–2.3 mm long; petals (2.5–) 2.6–3 mm long; filaments (3.7–) 4–5 (–5.2) mm long; style (3–) 5.5–6 mm long. Pods (9–) 12–14 (–15.3) cm long, (9–) 14–18 (–23) mm wide, 2–4 (–8) per capitulum, glabrous and slightly lustrous or with dense velutinous pubescence. Seeds 4.9–6.6 mm long, 3.5–4.6 mm wide.

REPRESENTATIVE SPECIMENS. **Mexico.** OAXACA: 25 km S of Sola de Vega, rd to Puerto Escondido, Sierra Madre del Sur, 16°02'N, 97°09'W, 12 Nov 1983, *Hughes 386* (FHO, K, MEXU); 2 km E of San Isidro Llano Grande, coast rd between Pinotepa Nacional and Puerto Escondido, 15°59'N, 97°16'W, 9 Mar 1985, *Hughes 580* (FHO, K, MEXU); 10 km N of Candelaria, 40 km N of Pochutla, rd to Oaxaca, 15°51'N, 96°28'W, 11 Feb 1987, *Hughes 846* (FHO, K, MEXU); immediately S of El Arenal, 10 km E of Playa Coyula, nr the Pacific coast, 15°44'N, 96°01'W, 14 Feb 1987, *Hughes 854* (FHO, K, MEXU); 6 km W of Pinotepa Nacional, rd to Acapulco, 16°21'N, 98°03'W, 21 Feb 1987, *Hughes 873* (FHO, K, MEXU); rd N from Juchitán to Acayucan 5 km N of Matías Romero, low windswept hills, Tehuantepec isthmus, 16°56'N, 95°01'W, 12 Mar 1989, *Hughes 1304* (CR, FHO, K, MEXU, NY); 2 km inland from Pacific coast, 10 km E of Coyula, 20 km E of Puerto Angel, dry valley between Coyula and Bahía Santa Cruz, 15°47'N, 96°07'W, 27 Mar 1989, *Hughes 1340* (BR, FHO, K, MEXU, NY); 8 km SE of Cacahuatpec, 3 km NW of Ixcapa, 16°35'N, 98°10'W, 17 Apr 1976, *Sousa 5507* (MEXU); 14 km SE of Pinotepa Nacional, 4 km NW of Nuaxpaltepec, Jamiltepec, 16°21'N, 97°56'W,

3 Mar 1982, *Zárate 641* (MEXU); Revolución, 16 km NW of Palomares, rd to Tuxtepec, 17°10'N, 95°11'W, 23 Feb 1978, *Sousa 9240* (MEXU, MO, UC); "El Tigre," 2 km N of San Agustín Chayuco, Jamiltepec, 16°25'N, 97°49'W, 6 Apr 1982, *Tenorio 234* (CAS, MEXU, MO); 1.2 km N of jet to Vivero Guapinol towards San Agustín Chayuco, 24 km SE of Pinotepa Nacional, 16°19'N, 97°51'W, 22 Oct 1982, *Torres 1637* (CAS, MEXU, MO); Rancheria La Esmeralda, 6 km S of San Gabriel Mixtepec, 16°04'N, 97°04'W, 12 Feb 1976, *Sousa 5306* (MEXU); Acatlán, 1 km W of Tetela, Dto. Tuxtepec, 18°29'N, 96°27'W, 22 Dec 1978, *Sousa 10306* (CAS, MEXU, MO); 1 km E of Atoyaquillo, Putla, 16°49'N, 97°47'W, 22 Dec 1987, *Solano 70* (MEXU); 5 km W of Jamiltepec, 16°18'N, 97°52'W, 7 Dec 1978, *Sousa 9928* (CAS, MEXU, MO); 11 km N of Matías Romero, 4 km S of Piedra Blanca, 16°55'N, 95°03'W, 23 Feb 1978, *Sousa 9225* (MEXU, MO, UC); 6 km NW of Pinotepa Nacional, Dto. Jamiltepec, 16°23'N, 97°51'W, 22 Oct 1977, *Sousa 8453* (CAS, MEXU, UC); Río Pacine, 3 km NE of San Juan Guichicovi, Juchitán, 16°58'N, 95°04'W, 25 Mar 1988, *Torres 12018* (MEXU); 3 km N of Santa María Chimalapa, track to Paso Mactaspac del Río del Corte, 16°55'N, 94°41'W, 14 Nov 1984, *Hernández 589* (CAS, MEXU, MO); 3 km E of Ojo de Agua S of Sola de Vega, 16°24'N, 97°05'W, 9 Dec 1978, *Sousa 9986* (CAS, MEXU, MO).—VERACRUZ: N side of Cerro de los Metates, 25 Jun 1972, *Dorantes 1011* (F, MEXU); Salto de Agua, 11 km S of Santiago Tuxtla, 18°23'N, 95°20'W, 21 Mar 1967, *Sousa 3007* (MEXU); nr Plan del Río and Emiliano Zapata, 19°20'N, 96°38'W, 16 Sep 1982, *Villanueva 246* (NY); Salto de Eyipantla, 8 km from Sihuapan, nr San Andrés Tuxtla, 18°24'N, 95°12'W, 26 Jan 1978, *Calzada 4245* (F).

The name *istmensis* refers to the occurrence of this subspecies from the Pacific foothills of coastal Oaxaca across the Isthmus (*istmo*) of Tehuantepec to a restricted area around San Andrés Tuxtla in southern Veracruz. It is essentially a lowland subspecies of the dry deciduous tropical forest. Pods of subsp. *istmensis* are usually glabrous and slightly lustrous, but pods of trees from one population (*Hughes 854, 855, 1340*) from coastal Oaxaca, 20 km east of Pochutla near Coyula, have dense velutinous pubescence.

Leucaena leucocephala (Lam.) de Wit, *Taxon*. 10: 53. 1961. *Mimosa leucocephala* Lam., *Encycl.* 1: 12. 1783. *Acacia leucocephala* (Lam.) Link, *Enum. hort. berol.* 2: 444. 1822.—TYPE: specimen in Lamarck herbarium labeled "Mimosa latisiliqua," "Mimosa leucocephala" (holotype: P-LA, microfiche K!).

Variation within *L. leucocephala* was first noted by agronomists who were evaluating the performance of different accessions for fodder production in field trials (e.g., Hutton & Gray 1959; Brewbaker et al. 1972). Two main variants, based primarily on habit, degree of branching, and vigor were recognized: a shrubby, low growing, highly branched, seedy, and often weedy, variant designated the 'Common' or 'Hawaiian' type; and an erect, arborescent, little-branched, less seedy variant designated the 'Giant' or 'Salvador' type (Hutton & Gray 1959; Gray 1967; Brewbaker et al. 1972; Brewbaker 1980; Brewbaker, 1987).

Although it was realized from the start that the 'Giant' or 'Salvador' type corresponded to the type material of *L. glabrata* Rose (*Palmer 386* from the vicinity of Acapulco, Guerrero, Mexico) (e.g., González et al. 1967), Brewbaker (1980) initially treated *L. glabrata* as a synonym of *L. leucocephala* and only later alluded to the distinction of two formal varieties, var. *leucocephala* corresponding to the shrubby 'Common' or 'Hawaiian' type and var. *glabrata* corresponding to the 'Giant' or 'Salvador' type (Brewbaker 1987). The formal recognition of two infraspecific taxa within *L. leucocephala* was discussed by Zárate (1987), who raised their rank to subspecies and published the combination: *L. leucocephala* (Lam.) de Wit subsp. *glabrata* (Rose) S. Zárate. The two subspecies recognized by Zárate (1987) correspond directly to the agronomic 'types,' viz: subsp. *leucocephala* = 'Common' or 'Hawaiian' type; subsp. *glabrata* = 'Giant' or 'Salvador' type.

Zárate (1987) listed the characters, in addition to habit, degree of branching, and vigor, that distinguish subspecies *leucocephala* and *glabrata*. These included leaf size, leaflet size, pod and seed size, habit, and, most notably, vestiture of the shoot, leaf rachis, leaflet, and pod. Subspecies *glabrata* has larger leaves, leaflets, and pods, and is almost entirely glabrous, compared to the smaller leaves, leaflets, pods, and densely puberulent, canescent shoot, leaf rachis, and pods of subsp. *leucocephala*.

During recent exploration by Hughes and collaborators in northern Guatemala, an additional variant, which differs from both subspecies *leucocephala* and *glabrata*, was encountered in a localized area around the town of Ixtahuacán in the highlands of Huehuetenango. This variant has the small leaves, leaflets, and pods of subsp. *leucocephala*, but is glabrous like subsp. *glabrata*. This material is here described as a third subspecies.

Leucaena leucocephala* subsp. *ixtahuacana C. E. Hughes, subsp. nov.—TYPE: GUATEMALA. Huehuetenango: 1 km ENE of San Miguel, track running WSW from Ixtahuacán into the valley of the Río Cuilco, 15°23'N, 91°50'W, *Hughes et al. 1689* (holotype: FHO!; isotypes: distributed to: E, K, MEXU, MO, NY).

A *L. leucocephala* subsp. *leucocephala* ramulis, rachibus, foliolis fructibusque glabris differt.

Small tree, (3–) 5–7 m tall, bole 5–20 cm in diameter, arborescent with a short clear bole to 2 m high and a rounded compact crown. Leafy shoots glabrous. Leaves (10–) 13–16 cm long, 8–11 cm wide, petioles 13–23 mm long, glabrous, petiolar nectary 2–2.4 × 1.2–1.5 mm; rachis (5–) 7–12 long, glabrous, mucro 1.9–3.6 mm long, very sparsely puberulent; pinnae (4–) 6–8 pairs; pinnular rachis 5–8 cm long, glabrous; leaflets 16–20 pairs per pinna, 9–11 mm long, 2–2.6 mm wide, glabrous or very sparsely ciliate along leaflet margins near base. Capitula 12–17 mm in diameter at anthesis each with 110–120 flowers, in fascicles of 2–6; peduncles 15–19 mm long, glabrous. Flowers subtended by peltate bracts, 2.3–2.4 mm long; calyx 2.8–3.8 mm long; petals free at base, partially united above, 5–5.2 mm long; filaments 6.2–8.8 mm long; ovary 2–2.3 mm long; style 7.8–8.8 mm long. Pods (9–) 10–13 cm long, (13–) 15–17 mm wide, (3–) 6–12 per capitulum, linear-oblong, acute apically, 8–14-seeded, valves mid-reddish brown, glabrous and slightly lustrous. Seeds 8–9.6 mm long, 4.7–6.3 mm wide.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: 2 km SE of Tolimán rd to Ojo de Agua and Berriozábal, nr Motozintla de Mendoza, 15°19'N, 92°19'W, 10 Mar 1981, *Sousa 11827* (CAS, K, MEXU). **Guatemala.** HUEHUETENANGO: Huehuetenango, 10 Nov 1934, *Skutch 1631* (A); rd from Huehuetenango NW to La Mesilla, 10 km WNW of Colotenango, valley of Río Selegua, 15°27'N, 91°46'W, 30 Mar 1988, *Hughes 1132* (FHO, K, MEXU); rd W from Colotenango to Cuilco, 5 km W of Ixtahuacán, above Río Cuilco, 15°25'N, 91°48'W, 9 Apr 1991, *Hughes 1469* (EAP, FHO, K, MEXU, NY); 1 km ENE of village of San Miguel, track running WSW from Ixtahuacán, into valley of Río Cuilco, 15°23'N, 91°50'W, 28 Feb 1992, *Hughes 1689* (E, FHO, K, MEXU, MO, NY).

The characteristics and distribution of this subspecies remain poorly known. Further field exploration will be needed to assess whether this variant is as localized—in a small area of northern Guatemala and the immediate border zone in Mexico around Motozintla, largely in the valleys of the Río Cuilco and Río Selegua, in the Department of Huehuetenango and in Chiapas—as current collections

suggest. Subspecies *ixtahuacana* is named with reference to its very localized distribution centered on the small town of Ixtahuacán.

Leucaena magnifica (C. E. Hughes) C. E. Hughes, comb. et stat. nov. *Leucaena shannonii* subsp. *magnifica* C. E. Hughes, Kew Bull. 46: 547. 1991.—TYPE: GUATEMALA. Chiquimula: Llano Grande, 1.5 km SW of Quetzaltepeque, rd towards Esquipulas, 14°37'N, 89°27'W, 26 Feb 1988, *Hughes 1093* (holotype: FHO!; isotypes: K! MEXU!).

Leucaena magnifica was first discovered in 1984 (Hughes 1986) and originally described as a subspecies of *L. shannonii* (Hughes 1991). It is here recognized as a species distinct from *L. shannonii* based on its consistently once-branched, as opposed to unbranched, flowering shoots. Taking this character alone *L. magnifica* is clearly diagnosable by its unique combination of character states and thus comprises a “phylogenetic species.” Evidence from cpDNA and isozymes also supports recognition of *L. magnifica* as a species distinct from *L. shannonii*. Harris et al. (1994), in their cpDNA analysis, showed that *L. magnifica* was the sister species to *L. shannonii*, a relationship supported in 85% of bootstrap replicates, and that they were separated by four autapomorphic fragment changes, two of which were unique. Chamberlain et al. (1996) analyzed isozyme variation across the *L. shannonii* alliance. Using the population aggregation analysis method of Davis and Nixon (1992) to delimit phylogenetic species, they showed that *L. magnifica* was separated from *L. shannonii* by the fixed occurrence of allele A of the Per-1 isozyme system. In addition, *L. magnifica* and *L. shannonii* differ in a number of quantitative characters (Hughes 1991): *L. magnifica* has larger leaves with more pairs of pinnae, more pairs of leaflets, larger leaflets, larger flowers, more flowers per capitulum, larger pods and seeds, pods with dense velutinous pubescence, that are often deep maroon when unripe, and more pods per capitulum than *L. shannonii*.

Leucaena matudae (S. Zárate) C. E. Hughes, comb. et stat. nov. *Leucaena esculenta* (Sessé & Mociño ex DC.) Benth. subsp. *matudae* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 134. 1994.—TYPE: MEXICO. Guerrero: Casa Verde, nr Venta Viejo in the Cañón de Zopilote, “guaje chismoso,” 17°50'N, 99°34'W, 12 Dec 1978, *Halbinger 288* (holotype: MEXU!, isotypes: ENCB! MO! NY!).

Leucaena matudae was originally described as a subspecies of *L. esculenta* (Zárate 1994), but is here raised to species rank in recognition of its clear morphological and molecular distinction from *L. esculenta*. Although cladistic analyses of morphology (Hughes, in press) and cpDNA (Harris et al. 1994) support the placement of *L. matudae* in the *L. esculenta* alliance, *L. matudae* is distinguished by a number of discrete character states. Most notably, the petiolar nectary of *L. matudae* is stipitate, erect, cylindrical, and quite unlike the large sessile, elongate, concave, crateriform nectary of *L. esculenta*. In addition, *L. matudae* may be distinguished by its terete, as opposed to the angular, ridged shoots of *L. esculenta*, fewer pinnae pairs and leaflets per pinna, fewer flowers per capitulum, smaller, weakly constricted pods which are partitioned between the seeds, and oblique alignment of seeds in the pods. Although *L. matudae* shares the same bark type as the remaining species in the *L. esculenta* alliance (thick corky bark with a single

periderm, a pale metallic grey surface, and deep blood-red inner bark), the bark surface pattern in *L. matudae* is quite distinct and unique within the genus in having a scalloped surface resulting from shedding of small circular plates. Zárate (1994) mentioned use of the bark for medicinal purposes and attributed the unusual surface pattern to local harvesting of bark for medicinal use, but given that there is no evidence of harvesting in most areas, that the patterns are extremely regular, and that they are found on inaccessible branches as well as boles, it seems clear that this is the natural state. Finally, Harris et al. (1994) emphasized the clear distinction in cpDNA between *L. matudae* (treated by them as *L. esculenta* subsp. *matudae*) and *L. esculenta*. Recognition of *L. matudae* as a separate species is thus amply justified by a suite of discrete character states that separate it from *L. esculenta*.

Leucaena confertiflora S. Zárate, *Anales Inst. Biol. Univ. Nac. Auton. México, Bot.* 65: 148. 1994.—TYPE: MEXICO. Oaxaca: Matatlán, Cerro Nueve Puntas nr shortwave relay mast, 5 km S of Matatlán, 16°49'N, 96°21'W, 2050 m, 22 Jan 1980, Zárate with Reid 428 (holotype: MEXU!).

The material of *L. confertiflora* from San Pedro Chapulco, Puebla, Mexico, and the surrounding area near the village of Azumbilla and the northern fringes of the Sierra Zongolica was observed by Zárate (1994) to differ in the shape of the extrafloral petiolar and leaf rachis nectaries from material from the remainder of the distribution further south in Puebla and Oaxaca. This difference was used by Zárate (1994) to divide *L. confertiflora* into two subspecies: subsp. *confertiflora* with sessile, discoid or shallow crateriform, concave nectaries on the petiole and rachis, and subsp. *adenotheloidea* with stipitate, erect peg-shaped, cylindrical nectaries, usually occurring at the base of each pair of pinnae. Zárate (1994) discussed the lack of other distinguishing features between these two subspecies. While the nectary shape is clearly distinct at the extremes, and fixed in most areas, variation within populations and even within individuals has been observed. Firstly, material from the mountains north-west of Huajuapán de León, around Santa Catarina Zapocuila and Membrillos (*Hughes 1812*), has both gland types within populations indicating the presence of both infraspecific taxa in this area. Secondly, in the village of Santa Catalina Oxolotepec, in the Sierra Zongolica, both nectary types and intermediate forms are found within the cultivated material there and even on single individuals (*Hughes 1616, 1731, 1799*). Inconstancy of the nectary shape in some areas and the lack of other distinguishing features justify treatment at varietal rather than subspecific rank necessitating the new combination:

Leucaena confertiflora S. Zárate var. ***adenotheloidea*** (S. Zárate) C. E. Hughes, stat. nov. *Leucaena confertiflora* subsp. *adenotheloidea* S. Zárate, *Anales Inst. Biol. Univ. Nac. Auton. México, Bot.* 65: 149. 1994.—TYPE: MEXICO. Puebla: San Pedro Chapulco, 13 km NE of Tehuacán on rd towards Orizaba, 18°36'N, 97°25'W, 2100 m, 7 Dec 1981, Zárate with Reid 610 (holotype: MEXU!).

Leucaena lanceolata S. Watson, *Proc. Am. Acad. Arts* 21: 427. 1886.—TYPE: MEXICO. Chihuahua: Batopilas, Hacienda San Miguel, SW Chihuahua, 27°53'N, 108°26'W, Sep 1885, *Palmer 6* (holotype: NY!; isotypes: UC! US! GH!).

Leucaena lanceolata is an extremely variable species across its extensive and largely continuous distribution along the Pacific coast of Mexico from Sonora to Chiapas, with outlying occurrences in Baja California and Veracruz. Zárte (1994) described the new subspecies *sousae* to account for the variation encountered towards the southern limits in Michoacán and Oaxaca. A detailed study of morphological variation within *L. lanceolata* was undertaken to investigate the basis for this subdivision. This study shows that there are no clear discontinuities in quantitative leaf or pod traits across the range of *L. lanceolata* that might be used to divide the species unambiguously. Nevertheless, there is some evidence to support the recognition of subsp. *sousae*. Variation in leaflet and pod traits shows some correlation with geography and with leaflet and pod vestiture, and two broad groups can be distinguished as recognized by Zárte (1994). Moreover, Harris et al. (1994) mentioned the existence of two cpDNA plastome types within *L. lanceolata* across the seven accessions included in that study. Further analysis shows that cpDNA variation within *L. lanceolata* is not perfectly correlated with the morphological variation, although the two accessions of subsp. *sousae* did group together, lending some support for recognition of that taxon. Pending more detailed analysis and given the lack of clear discontinuities, subsp. *sousae* is here demoted to varietal rank:

Leucaena lanceolata* var. *sousae (S. Zárte) C. E. Hughes, stat. nov. *Leucaena lanceolata* subsp. *sousae* S. Zárte, *Anales Inst. Biol. Univ. Nac. Auton. México, Bot.* 65: 117. 1994.—TYPE: MEXICO. Oaxaca: 17 km WNW of Puerto Escondido, Dtto. Juquila, 15°57'N, 97°13'W, 21 Oct 1976, *Sousa* 6390 (holotype: MEXU!, isotype UC!).

Leucaena rekoii Britton & Rose, *Fl. N. America.* 23: 122. 1928.—TYPE: MEXICO. Oaxaca: nr Pochutla, close to the Pacific coast, 15°44'N, 96°28'W, 28 Sep 1917, *Reko* 3632 (lectotype, here designated, flowering shoot and leaves only: US!).

Discontinuities in the morphological variation within *L. lanceolata* are blurred by three exceptions to the general trends in leaflet and pod size and vestiture identified as the basis for recognition of var. *sousae*. Firstly, pods which are generally pubescent in var. *lanceolata* and glabrous in var. *sousae*, are exceptional in several areas. In Baja California, pods are glabrous, whereas quantitative traits indicate that this material belongs with var. *lanceolata* (see *Hughes* 1544). In the transition area between var. *sousae* and var. *lanceolata* in a well-defined zone around Bahía de Santa Cruz in south-central Oaxaca (see *Hughes* 841, 587, 835, 836), pods are pubescent, while the large leaflets and pods indicate that this material belongs with var. *sousae*. At inland, slightly higher-elevation, drier sites in southern Oaxaca (see *Hughes* 556, 1345, 1724) pods are glabrous, with an unusual glossy or 'basted' surface. Secondly, this same material from inland Oaxaca from the Municipios of San Bartolo Yautepec, Jalapa de Marqués, and Santiago Lachiguirí also has wider pods than typical for var. *lanceolata*, and pods which are slightly falcate. Finally, in the coastal zone 20–40 km west of Playa Azul in Michoacán, it is difficult to separate the two varieties, which appear to grow together there.

These difficulties were recognized by Zárte (1994) in his discussion of var. *sousae* (as subsp. *sousae*) when he stated that although readily distinguished at the type locality, in other areas it may be more difficult to define. Zárte (1994)

attributed this to his hypothesis that it is of hybrid origin between *L. macrophylla* (*L. macrophylla* subsp. *nelsonii* sensu Zárate) and *L. lanceolata* var. *lanceolata*, although he did not provide conclusive evidence to confirm this hypothesis.

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